

THE POMARINE JAEGER AS A BROWN LEMMING PREDATOR IN NORTHERN ALASKA

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THE population fluctuations of many arctic predators, both avian and mammalian, are associated with changes in the numbers of their major prey, the several species of arctic lemmings.

Pitelka, Tomich, and Treichel (1955a) reported that the breeding densities of avian predators near Barrow, Alaska from 1951 to 1953 were correlated with lemming abundance. Their work confirmed that the Pomarine Jaeger (*Stercorarius pomarinus*) is a major lemming predator in northern Alaska and documented qualitatively the relationship of this species with the population cycle of the brown lemming (*Lemmus trimucronatus*) in that region. They also pointed out the desirability of quantifying the relationship between the two species. Accordingly the major objective of my study was an attempt to define the relationship between the populations of the Pomarine Jaeger and the brown lemming quantitatively, in order to determine the role of avian predators in the lemming cycle. In this paper I will discuss the food habits, nesting density, and reproductive success of the jaeger population and try to assess the impact of their predation on the brown lemming population. The interactions of populations in a simple system involving a single prey species and several avian predators should contribute to understanding of predator-prey relationships in general, in addition to the specific question of the role of predation as a possible cause of the lemming cycle itself.

My study was conducted for five seasons in northern Alaska through a complete lemming cycle, beginning with a high lemming population in 1956 and terminating with a second lemming high in 1960. Most of the field work was done at Barrow, although data were also obtained at Pitt Point, Wainwright, and Cape Sabine (Fig. 1). Additional observations were made in 1954 and 1955 when I was employed at Barrow by the U. S. Geological Survey. I was at Barrow briefly in the summer of 1953 and witnessed the lemming high of that year.

ENVIRONMENT

Barrow is at the northern tip of Alaska at approximately 70°N. Latitude. It is at the apex of a wide triangular coastal plain that is 400 miles from east to west and 80 miles from north to south at its widest longitude through Barrow (Fig. 1).

This paper is concerned with the portion of the coastal plain within which the brown lemming population cycles regularly, as well as with a coastal strip

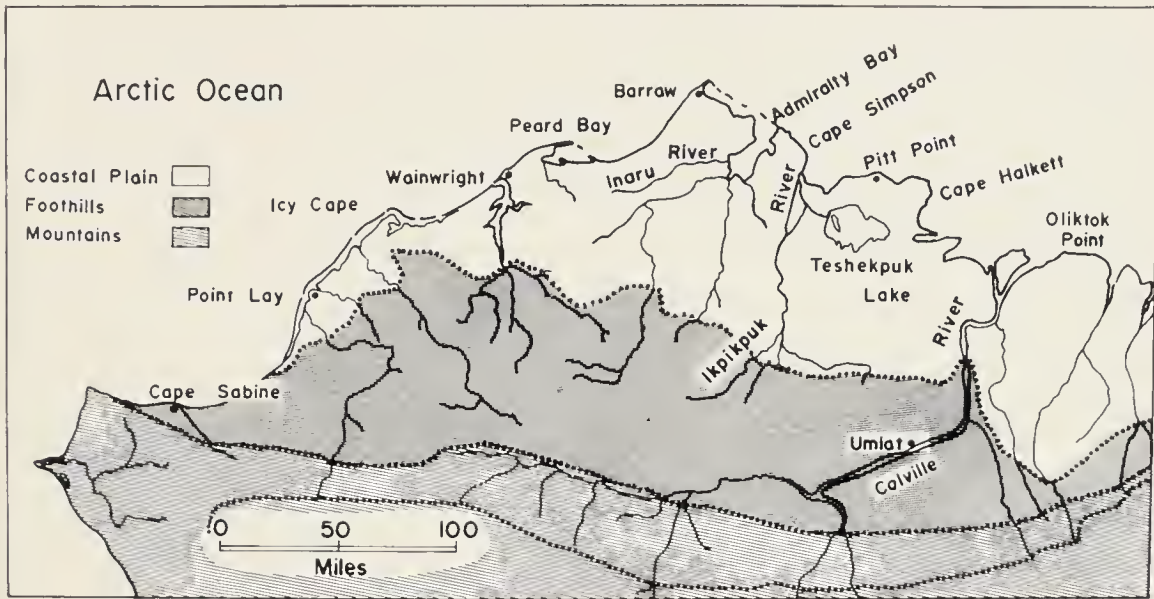


FIG. 1. Map of northern Alaska with place names mentioned in the text.

usually less than five mile wide, extending from Cape Sabine on the West to Oliktok Point on the east, within which the brown lemming population fluctuates irregularly. The portion of the coastal plain within which lemming highs regularly occur is triangular and extends 80 miles east and west of Barrow and 25 to 30 miles inland at its widest point south of Barrow. The environmental description applies to the area thus defined.

The northern part of the north Alaskan coastal plain is a region of low relief, extensive marshy areas, meandering streams, and numerous lakes and ponds. The development of mature drainage has been impeded by the level topography and by underlying permafrost. Twenty per cent of the area is covered by lakes (Spetzman, 1959) and more than 50 per cent is covered with standing water (Black and Barksdale, 1949).

The vegetation of this region, as of tundra generally, is low. The vegetation on mesic and wet sites at the end of the growing season averages approximately six inches in height. The vegetation on dry sites is lower, and on a few favourable wet sites it can be several inches taller.

Marsh areas dominated by *Carex* species, especially *Carex aquatilis*, cover approximately one-third of the land area under consideration (Thompson, 1955b). Marsh usually occurs on a saturated peat substrate, often with one to three inches of standing water. Marsh vegetation occupies the saucer-like depressions of low-center polygons (Thompson, op. cit.) as well as extensive marshes in partly drained lake basins and around the edges of ponds and lakes. Elevated drier sites typically contain a poorly developed tussock-heath tundra association (Britton, 1957 and Spetzman, 1959). This association is

essentially a simple mat of sedges and grasses with a minor element of prostrate willow shrubs, heath species, mosses and lichens. *Eriophorum vaginatum*, which further inland forms large tussocks, is here reduced in stature and inconspicuous. The most common heath elements are *Ledum groenlandicum*, *Vaccinium vitis-idaea*, and *Cassiope tetragona*.

The climate of the arctic coast of Alaska is severe. Winters last nine to ten months and are cold. Summers are short and cool. The average annual temperature at Barrow is 10.1°F. The mean temperature for February, the coldest month, is -18.1°F, and for July, the warmest month, it is 40.0°F. The mean minimum temperature is above freezing from late June to early August. The tundra is free of snow for the latter part of June, July, August, and early September. Frost is possible in all months. The mean annual precipitation averages 4.1 inches at Barrow. The sun is above the horizon continually for 87 days from 9 May through 4 August.

Cape Sabine is in the northern foothills of the Brooks Range where they reach the coast (Fig. 1). The study area, about one mile inland, is characterized by long parallel rocky ridges separated by broad shallow swales. The vegetation is much more complex than in the portion of the coastal plain described above. Well developed tussock-heath tundra covers the slopes and luxuriant *Carex* marsh occurs in the swales. Marsh vegetation here is dense and is 14 to 16 inches tall by mid-July. The Pomarine Jaegers which bred in the area nested in the swale bottoms.

BACKGROUND

A review of the recent history of the brown lemming population in northern Alaska, and some information on lemming biology and predator biology are necessary for understanding the spatial and temporal aspects of the breeding ecology of the Pomarine Jaeger.

The brown lemming population of northern Alaska has been studied continuously since 1949. Details of population fluctuations and other aspects of lemming ecology are in Rausch (1950), Thompson (1955a, 1955b, 1955c), and Pitelka (1957a and 1957b).

Lemming highs are characteristic of coastal tundra in northern Alaska (Pitelka, 1957a), and seem to be confined to the northern portion of the coastal plain, already described, where, as a result of climatic modification by the arctic ocean, the tundra vegetation is simpler than tundra inland. Two lemming species occur in this area, the brown lemming and the collared lemming (*Dicrostonyx groenlandicus*). The latter species is relatively rare and locally distributed, so that the brown lemming is the only significant microtine rodent in this coastal area.

Up to the termination of this study in 1960 general lemming highs were observed in northern Alaska in 1949, 1953, 1956, and 1960. A general, moderate lemming population occurred in 1952, and low populations occurred in 1950, 1951, 1954, 1955, 1957, 1958, and 1959.

In 1956 maximum lemming density occurred in a triangular area of 1,200 to 1,500 square miles extending south from Barrow 25 miles to the Inaru River, east 60 miles to Cape Simpson, and west 70 miles to Peard Bay. About the periphery of this area was a region of lower population density which was approximately ten miles wide on the western and southern edges but extended 30 miles eastward of Cape Simpson nearly to Pitt Point (Pitelka, 1957a).

In 1960 the western and southern borders of the lemming high were approximately the same as in 1956; but, lemmings were scarce in the area between Admiralty Bay and Cape Simpson and east to the Ikpikpuk River. Eastward from there to Oliktok Point there was a moderately high lemming population occupying a narrow region along the coast. The extent of the 1960 high was also estimated to be 1,200 to 1,500 square miles. Accurate information on the extent of the 1953, and 1949 highs is not available. The evidence suggests that they were confined to the area of the 1956 high.

There were two localized highs of *Lemmus* in northern Alaska in 1957 in areas peripheral to the main area discussed above and out of phase with it. The more extensive of these was centered at Pitt Point approximately 80 miles east of Barrow. Its exact extent was not determined; but it was known to occupy the tundra between Teshekpuk Lake and the Arctic Ocean. Its western boundary was near Longitude $153^{\circ}45' W$. It did not reach the Kogru River (Longitude $152^{\circ}30' W$), but the eastern limits were not determined more precisely. This lemming high occupied an area of 250 to 400 square miles.

A second lemming high occurred in 1957, 90 miles west of Barrow at Wainwright, and extended at least 5 miles inland on the east side of Kuk Inlet. Its extent was not otherwise determined.

The tundra vole (*Microtus oeconomus*) occurs regularly as far north as the northern foothills of the Brooks Range and the southern coastal plain. In that area its population fluctuations are apparently restricted, but occasional local population highs are known to occur. A coastal population of this species coexisting with four other microtine rodents was studied at Cape Sabine from 1957 to 1959 (Childs, 1959). The *Microtus* population built up rapidly in the summer of 1958 and reached a high level at the end of that season. In the summer of 1959 the *Microtus* population was still high, and four pairs of Pomarine Jaegers bred there for the first time. The extent of this high is not known, but it appeared to be local and probably occupied less than 25 square miles.

To summarize: In northern Alaska in 12 seasons from 1949 to 1960 widespread lemming highs occurred four times, a widespread moderate lemming population once, and the lemming population was low in seven seasons. In 1957 there were two local highs at Pitt Point and Wainwright.

The interval between the general lemming highs since 1949 has been three to four years. The amplitude of the fluctuations is large, but lemming density varies between peak years, and estimates of the magnitude of the fluctuation differ greatly. Thompson (1955*b*) estimated that there was a 400-fold increase from the low of 1950 to the 1953 peak at Barrow. Krebs (1964) estimated a 25- to 50-fold increase in the winter preceding the 1960 lemming high at Baker Lake, N.W.T., and a two- to three-fold increase during that summer, following a brief decline at melt-off in June. Shelford (1943) estimated an increase of 800- to 1,000-fold in the lemming cycle at Churchill, Manitoba.

Predators are not evident for two years following a decline from a high. Moderate numbers of lemmings are present either early or late in the third summer of a four-year cycle, and avian predators may exploit the third-year population if lemming density is high enough in the spring.

Although lemmings, like other microtines, sometimes breed in the winter, at Barrow when the snow cover melts in June the lemming population consists mostly of nonbreeding adult animals. Synchronous breeding in the population begins immediately and a large summer generation of lemmings emerges in mid-July. Breeding continues through the summer, and the first summer litter may produce a second generation in August or September. For additional information on the biology of the brown lemming in northern Alaska, the reader is referred to the papers of Rausch, Thompson, and Pitelka cited previously.

Five species of avian predators may be associated with the lemming high. They are the Pomarine Jaeger, the Snowy Owl (*Nyctea scandiaca*), the Parasitic Jaeger (*Stercorarius parasiticus*), the Short-eared Owl (*Asio flammeus*), and the Glaucous Gull (*Larus hyperboreus*). Significant mammalian predators are the least weasel (*Mustela rixosa*) and the arctic fox (*Alopex lagopus*). This study was concerned with the Pomarine Jaeger, but an attempt will be made to assess the total predation impact on the lemming population.

The breeding biology of the Pomarine Jaeger, in northern Alaska has been summarized by Pitelka, Tomich, and Treichel (1955*b*). The Pomarine Jaeger is a moderately large predator on its nesting grounds. Females collected in northern Alaska average 745 grams in weight and males 648 grams. Pomarine Jaegers arrive on the tundra in late May and early June. In breeding years they establish large all-purpose territories. The normal clutch of two eggs is laid in an unlined scrape on the tundra in mid- to late June. The chicks emerge

in mid-July and begin to fly in the last half of August. Adults and young depart in late August or early September.

GENERAL METHODS

Breeding jaegers are easily watched and censused because they are both conspicuous and aggressive and because tundra vegetation offers negligible interference with observation. At Barrow the study area was systematically traversed using a tracked vehicle, a wcaasel. Nests were staked, and the location of nests and territorial pairs was plotted on an outline map traced from aerial photographs. By continually rechecking the location of nests in relation to neighboring nests and landmarks, considerable accuracy was eventually obtained in maps of nest distribution. In 1956 and 1960 the nests on part of the study area were mapped with an alidade and plane-table. Censuses were repeated regularly in the season to determine population trends and breeding success. In areas away from Barrow censusing was done on foot, and pair and nest locations were marked on aerial photographs carried in the field.

The area censused differed between years depending on jaeger density. Thus, at Barrow in years of maximum jaeger density the study area was 5.75 and 6 square miles, while in years of low jaeger density about 15 square miles were censused. The size of the area studied is given with data on breeding density.

For feeding and growth studies nests were encircled with a fence 30 feet long and 12 inches high making an enclosure about 9 feet in diameter. Nine nests were enclosed at Barrow in 1956, one in 1959, and 15 in 1960. One nest was enclosed at Cape Sabine in 1959. When nests were fenced during the incubation period the adults returned to the eggs in minutes and fed the chicks normally when they hatched. Chicks fenced after hatching usually died because the adults did not feed them properly. As jaeger chicks cannot jump, they were not able to escape from the enclosure until they could fly. The enclosed nests were visited at regular intervals, the chicks weighed with a beam balance, and regurgitated pellets and other food remains collected.

Regurgitated food remains were softened in detergent and water. Jaws, skulls, femurs, and pelvises of small mammals, all identifiable remains of birds, and all other food items were picked out. The residue was floated in water so that insect fragments and other small remains were recovered.

The method of analysing the food remains depended on their condition. When pellets were intact, food items were recorded as the percentage of occurrence in the total number of pellets. When regurgitated food material was trampled or picked apart by the jaegers and individual pellets were not recognizable, food items were analysed as the occurrence in the total number of prey items. The number of lemmings and other vertebrate prey was the number of the most numerous bone element, usually the right or left jaw of lemmings. Only the occurrence of food items such as insect remains and egg-shell fragments was recorded for each sample.

Sex ratios of the pelvises removed from all pellets were determined. Separation of male and female pelvises more than 20 mm along the ilium-ischium axis on the basis of their shape is readily done on museum specimens (Dunmire, 1955). However, the most obvious difference between the male and female pelvis is the backward extension of the pubis of the female which gives the posterior border of the pelvis a sloping contour rather than the rounded contour of the male. This part of the female pelvis is thin and mechanical action of digestion often breaks off the pubo-ischial corner, causing the specimen to resemble a male pelvis.

The following criteria were used in addition to shape to distinguish the sexes. All pelves with a least pubic width of 0.7 mm or less were considered female, and all with a least pubic width of 1.00 mm or more were considered male. This separation, based on the results of measuring pelves of 50 males and 50 female museum specimens, can be done with 2 per cent error. The 24 per cent of the pelves with least widths of 0.8 and 0.9 mm were classified on morphological grounds, or rejected if a comfortable decision could not be made.

Two Pomarine Jaeger chicks were raised from hatching at the laboratory in 1960. Two partly grown chicks brought in from the tundra gave additional data on food consumption.

The chicks were placed outdoors in a large cage, eight by eight feet by ten feet high at the age of eight and nine days. Hence they were exposed to natural ambient temperatures, and had much freedom of activity. Records were kept of their daily weight and food consumption.

Systematic observations were made on frequency of feeding of breeding adults.

In 1957 and 1958, nonbreeding jaegers along the ocean near Barrow and Wainwright were collected by Eskimos. The specimens were frozen at the Arctic Research Laboratory, and processed at the end of the season for data on stomach contents, weight and reproductive condition.

Further details on methods will be given where they are appropriate.

RESULTS

Food habits of the jaeger.—The Pomarine Jaeger utilizes a large variety of food on its breeding grounds, although most items occur rarely in its diet, and there are few foods which it obtains in quantity. The very specialized adaptations of the Pomarine Jaeger as a predator are apparent when a distinction is made between the ability of the bird to obtain enough food for survival in nonbreeding years and its ability to feed itself and also raise a brood of chicks.

Nonbreeding populations of Pomarine Jaegers were sampled at Barrow and Wainwright in the low lemming years of 1957 and 1958. The variety of food items in the sample of 56 stomachs (Table 1) suggests that this jaeger is largely opportunistic in its food gathering and takes anything available.

Microtine rodents occurred in 41 per cent (23) of the stomachs, and birds were in 25 per cent (14) of them. Four of five shorebirds were Red Phalaropes (*Phalaropus fulicarius*) and one was a calidrine sandpiper, either *Erolia melanotos* or *E. alpina*. Remains of large birds were mostly unidentified, but included one ptarmigan. Two of 11 bird eggs were Red Phalarope. Carrion included caribou (*Rangifer tarandus*) and one seal (*Phoca* sp.). Marine invertebrates were unidentified squid, polychaete worms, and unidentifiable remains.

It appears from this analysis that jaegers were foraging over the tundra, along the ocean shore, and in the native villages. Caribou and seal remains were probably found near the villages. The marine invertebrates were prob-

TABLE 1
 FOOD OF NONBREEDING POMARINE JAEGERS, 1957 AND 1958

Food items	Number of stomachs	Per cent occurrence
Microtine rodent	23	41
Avian	14	25
Carrion	8	14
Bird egg	11	20
Insect	5	9
incidental in stomach	3	5
predominant in stomach	2	3
Fish	7	12
Marine invertebrate	2	3
Number of stomachs	56	

ably picked up on the beach as I have never observed jaegers robbing other birds of their food near Barrow and Wainwright, as has been frequently described by observers in temperate areas (see Bent, 1921). The only locality at which I did observe this behavior in northern Alaska was at Cape Sabine where there were a large number of Black-legged Kittiwakes (*Rissa tridactyla*); and even there it was uncommon.

Breeding populations were sampled by analysing regurgitated pellets collected on the tundra at Barrow in 1956, 1959, 1960, and at Pitt Point in 1957. Pellets were also collected from chick enclosures at Barrow in 1956, 1959, and 1960, and at Cape Sabine in 1959. Pellets of the current season were distinguished by dried mucus on their surface.

Two of these five jaeger populations were of maximum density (Barrow, 1956 and 1960), one was moderately dense (Pitt Point, 1957), and two were very sparse (Barrow and Cape Sabine 1959). Microtine rodents make up the bulk of the food utilized by all of these populations regardless of their breeding density (Table 2). At Barrow and Pitt Point *Lemmus* is the predominant microtine, *Dicrostonyx* occurs very rarely. *Microtus oeconomus* was the exclusive microtine prey at Cape Sabine.

Food other than microtine rodents is more than 10 per cent of the prey items only in the two sparse 1959 populations. in which it was 17 per cent at Barrow and 12 per cent at Cape Sabine. Birds were the most important prey category after microtine rodents. Bird remains consisted mostly of shorebirds, predominantly chicks, and a few ducklings and passerine birds. Remains of

TABLE 2
FOOD OF BREEDING POMARINE JAEGER POPULATIONS

Food item	Barrow		Pitt Point	Barrow	Capc Sabine
	1956	1960	1957	1959	1959
Total microtine	98.6 ^a	97.8 ^b	100 ^a	100 ^a (83) ^b	88 ^b
Other food	8.5	2.2	3	27 (17)	12
Bird	0.9	1.9	1	9 (7)	12
Bird egg	1.2	3	2	12 (10)	
Fish	0.2	0.3		3 (3) ^a	5 ^c
Insect (incidental)	6.2	1 ^c		3 (3) ^a	2 ^c
Number	432	2500	206	75 (89)	68

^a Per cent occurrence of food item in pellets.

^b Per cent occurrence of food item in total number of food items.

^c Number of occurrences in pellet samples; not included in total of prey items.

large birds, such as ducks, occurred very rarely. Fish and insects are unimportant and carrion, absent.

It seems justified to compare these results with the data from nonbreeding jaeger populations even though they are based on food remains in regurgitated pellets and the latter sample is based on analysis of stomach contents. All prey items found in stomachs were identified by undigestible parts such as feathers and bone, and all (except marine invertebrates) have also been found in pellets. Furthermore, items such as insect fragments, insect eggs and otoliths are readily found in pellets when they are examined thoroughly (see methods).

Nonbreeding populations utilized a much smaller proportion of microtine rodents and a larger proportion of birds than breeding populations did, and carrion and fish were significant components of their diet. Insects were most of the contents of three per cent of the stomachs, whereas they were always incidental in pellets of breeding populations.

These results confirm the great importance of lemmings in the diet of breeding jaegers. The relatively low number of prey items other than lemmings, also suggests that breeding jaegers are dependent on lemmings (or other microtine rodents) for sufficient food for successful breeding. The food habits of nonbreeding jaeger populations confirm this conclusion. Lemmings are the most important prey these birds obtain on the tundra; yet the importance of carrion and fish in their diet suggests that they foraged along the coast because they could not obtain sufficient prey from the tundra to survive or attempt to breed.

Jaeger breeding density and lemming density.—The fact that the Pomarine Jaeger is dependent on the lemming population for food poses problems of

adjustment of the jaeger population to a variable food supply. In order to maintain itself the jaeger population must exploit lemming populations efficiently when they are at densities high enough to support the predator's reproductive efforts. In any area, food will be adequate for jaegers in only one in three, or at best two in four years.

The Pomarine Jaeger responds to the lemming cycle by adjusting the fraction of its population which breeds. This adjustment is locally manifested by fluctuation of the jaeger's breeding density. The species cannot alter its clutch size in response to food supply as do many raptors, including the other major avian lemming predator, the Snowy Owl. Quantitative data on the total Pomarine Jaeger population are not available, but I would like to discuss breeding density changes and reproductive success in relation to lemming numbers.

The estimated density of *Lemmus* at the time of the snow melt-off is used to compare lemming densities between years, because this is a convenient, identifiable point at which to compare lemming populations, and because the jaegers are presumably responding to this initial number of lemmings when they begin breeding activities. The density estimates were made by Pitelka (Barrow) and myself (Barrow and Pitt Point) and are estimates with undetermined margins of error. The order of magnitude indicated by the difference between years is certainly a correct one (Table 3).

Information on changes in nesting density and breeding success of Pomarine Jaeger populations was obtained at Barrow from 1954 to 1960, from Wainwright and Pitt Point from 1956 to 1960, and Cape Sabine from 1957 to 1960. Spring lemming density estimates are only available from Barrow for all years and from Pitt Point in 1957. Information on jaeger breeding density and success in 1952 and 1953 are from Pitelka, Tomich, and Treichel (1955a).

In the nine seasons from 1952 to 1960 at Barrow the Pomarine Jaeger did not breed in three (1954, 1957, and 1958), small numbers bred in two seasons (1955 and 1959) and significant numbers of Pomarine Jaegers nested in only four of the nine seasons (1952, 1953, 1956, and 1960) (Table 3).

Other areas show similar variations in the breeding density of the Pomarine Jaeger. At Wainwright breeding occurred in only three of the five years, and breeding density was low each time. Pomarine Jaegers bred in only two of five years at Pitt Point. In 1957 a moderately high density of jaegers nested in response to a local lemming high; and in 1960, when the general lemming high of that year extended eastward past Pitt Point, a low density population of Pomarine Jaegers bred. Pomarine Jaegers bred only once at Cape Sabine from 1957 to 1960, and then only in very low numbers.

Comparison of spring lemming density with Pomarine Jaeger breeding

TABLE 3
BREEDING DENSITIES AND NESTING SUCCESS OF THE POMARINE JAEGER

Locality	Year	Spring <i>Lemmus</i> density (no./acre)	No. of pairs	Census area (square miles)	Density (pairs/ square mile)	Maximum density (pairs/ square mile)	Breeding success (per cent of eggs)
Barrow	1952	15-20	34	9	3.8	5-6 ^a	30-35 ^a
	1953	70-80	128	7	18.3	25-26 ^a	20-25 ^a
	1954	<1	0	—	—	—	—
	1955	1-5	2	15±	0.13	—	0
	1956	40-50	114	6	19.0	22-23	4
	1957	<1	0	—	—	—	—
	1958	≤1	0	—	—	—	—
	1959	1-5	3	15±	0.20	—	0
	1960	70-80	118	5.75	20.5	25	55
Wainwright	1956		3	2±	1-1.5	—	?
	1957		3-4	4	1.0	—	?
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4-5	?	2±	—	?
Pitt Point	1956		0	—	—	—	—
	1957	30-40	61	6	10.1	15	13
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4-5	1-2	—	—	?
Cape Sabine	1957		0	—	—	—	—
	1958		0	—	—	—	—
	1959		4 ^b	11	0.36	1 ^c	13
	1960		0	—	—	—	—

^a Estimates provided by F. A. Pitelka; see Pitelka, Tomich, and Treichel, 1955a.

^b This jaeger population nested in response to a high density of *Microtus oeconomus* for which no density estimate is available.

^c In suitable nesting habitat.

density at Barrow shows a clear correlation between the two (Table 3). The Pomarine Jaeger does not breed at spring lemming densities estimated to be below one per acre. Some breeding takes place at densities of approximately one to five lemmings per acre. Pomarine Jaeger density increases proportionately with lemming density until the mean maximum jaeger density of 18-20 pairs per square mile is reached. Three lemming highs (1953, 1956, and 1960) supported virtually identical mean Pomarine Jaeger densities near Barrow, though the magnitude of the lemming population peaks were different (Table 3, Fig. 2). The leveling of the Pomarine Jaeger's response curve at

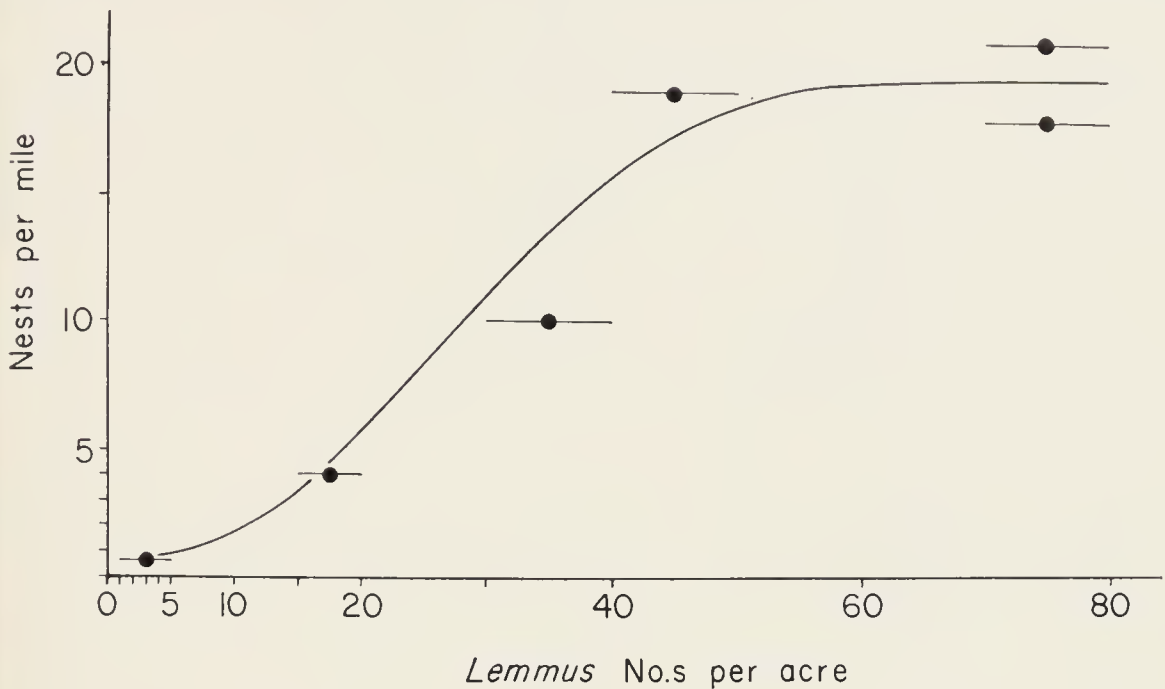


FIG. 2. Relationship between Pomarine Jaeger breeding density and the density of the spring brown lemming population.

high lemming densities suggests that different factors limit the breeding density of jaeger populations at high lemming densities than at low ones. Since the Pomarine Jaeger is strongly territorial and defends an all-purpose territory (Pitelka, Tomich, and Treichel, 1955a), territoriality appears to be the most likely mechanism limiting jaeger density. At jaeger densities below the maximum, food supply is probably limiting, but the question of how food supply acts to adjust Pomarine Jaeger breeding density is unanswered. The response may be related to different thresholds between young adults and more experienced breeders in the population. Fewer of the heavily striped jaegers, which are presumed to be younger individuals, are seen in the sparse breeding populations than are seen in the dense populations.

Breeding success of jaeger populations.—The apparent adjustment of Pomarine Jaeger breeding density to the lemming population level raises the question of the efficiency of the adjustment. The best criterion for judging its efficiency would seem to be the nesting success. If the adjustment of the jaeger's breeding density were efficient at all lemming densities, it should result in a relatively consistent level of reproductive success. In fact, reproductive success has not been constant (Table 3). Breeding success has tended to be low at low nesting densities (Barrow, 1955 and 1959, Cape Sabine, 1959), and low to moderate at intermediate densities (Barrow, 1952 and Pitt Point, 1957). At maximum density, breeding success at Barrow has ranged from

TABLE 4
SIZE CLASSES OF LEMMING FEMURS AND MEAN LEMMING WEIGHTS PER CLASS

No.	Size class (mm)	N	Mean wt. (g)	Weight factor (g)
1	<10	2	8.4	8.0
2	10-15	77	24.8	25.0
3	15-19	8	64.8	65.0
4	>19	22	89.1	90.0

almost complete failure (1956) to moderate success (1953) to high success (1960). The highest breeding success was achieved at high nesting densities.

The maximum populations must contribute most of the recruitment to jaeger numbers, as their large areal extent suggests that they involve a large proportion of the total jaeger population. Yet, breeding success was dramatically different in the two dense jaeger populations at Barrow in 1956 and 1960. Success in those years was clearly related to food supply. In 1956 the lemming population declined during the season (Pitelka, MS) and by late July was not sufficient to sustain the jaegers. Many of the chicks starved and those which did not die of starvation were killed by snow and cold weather on 9 and 10 August. The estimated four per cent success of total eggs laid is generous. In contrast, lemmings remained abundant all through the 1960 season (Pitelka, MS), and chick survival (55 per cent) was the highest recorded.

The sparse breeding populations of the jaeger probably do not contribute significantly to recruitment because of the small fraction of the population which breeds and the low success usually realized. In years when few jaegers breed, nonbreeding jaegers forage on the tundra singly or in large flocks. Breeding failure of jaegers frequently results from interference by these nonbreeding birds, or by nonbreeding Snowy Owls.

These data suggest that the territorial breeding system of the Pomarine Jaeger has evolved to enable the jaeger to limit its exploitation of high populations of lemmings so that the probability of significant reproductive success is increased.

Effect of jaeger predation on the lemming population.—Predators affect the numbers of the prey population directly by the number removed, and indirectly by altering the age and sex structure of the population and, hence, the future course of its dynamics. Four criteria were used to assess the impact of the Pomarine Jaeger on the brown lemming population. They are: (1) the size classes, and hence reproductive status of the removed population; (2) the number of prey taken; (3) the sex ratio of the removed population; and (4)

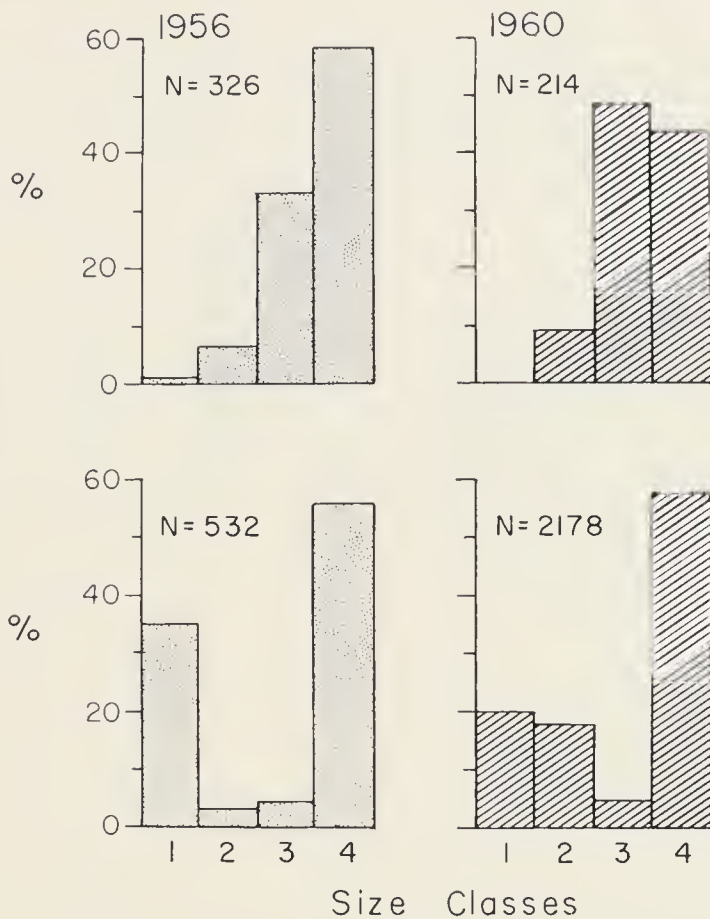


FIG. 3. Size classes of lemming femurs in adult jaeger pellets (top) and penned jaeger chick pellets (bottom) in 1956 and 1960.

the timing of the predator impact in relation to the annual population cycle of the prey.

(1) *Size classes of lemmings taken.*—The impact of jaeger predation on the lemming population can be partly assessed if we know the age groups of the prey affected. Size is used here as an approximate indicator of age and reproductive status. The femurs were sorted into four arbitrary size classes (Table 4). The mean weight of each class was determined from skeletons of animals of known weight (Table 4).

The size classes of lemmings taken early in the season are indicated by the frequency distribution of femurs from adult jaeger pellets from 1956 and 1960 (Fig. 3). Pellets were collected through the season in 1956, but most were collected in late May and June and most collected later were probably from the spring as indicated by the low percentage of the two smallest lemming size classes. The 1960 sample was collected in June. In both seasons most lemmings taken in spring are in classes 3 and 4, which are small and large adult animals.

The size classes of prey taken in the latter part of the season were obtained from chick pellets from enclosed nests. In 1956 chick pellets were collected from 21 July to 9 August and in 1960 from 12 July to 17 August. Large adult lemmings were predominant in both years (Fig. 3). The most significant difference between the two seasons is the occurrence of size classes 1 and 2. The mean weight of the smallest size class is 8.4 g (Table 4).

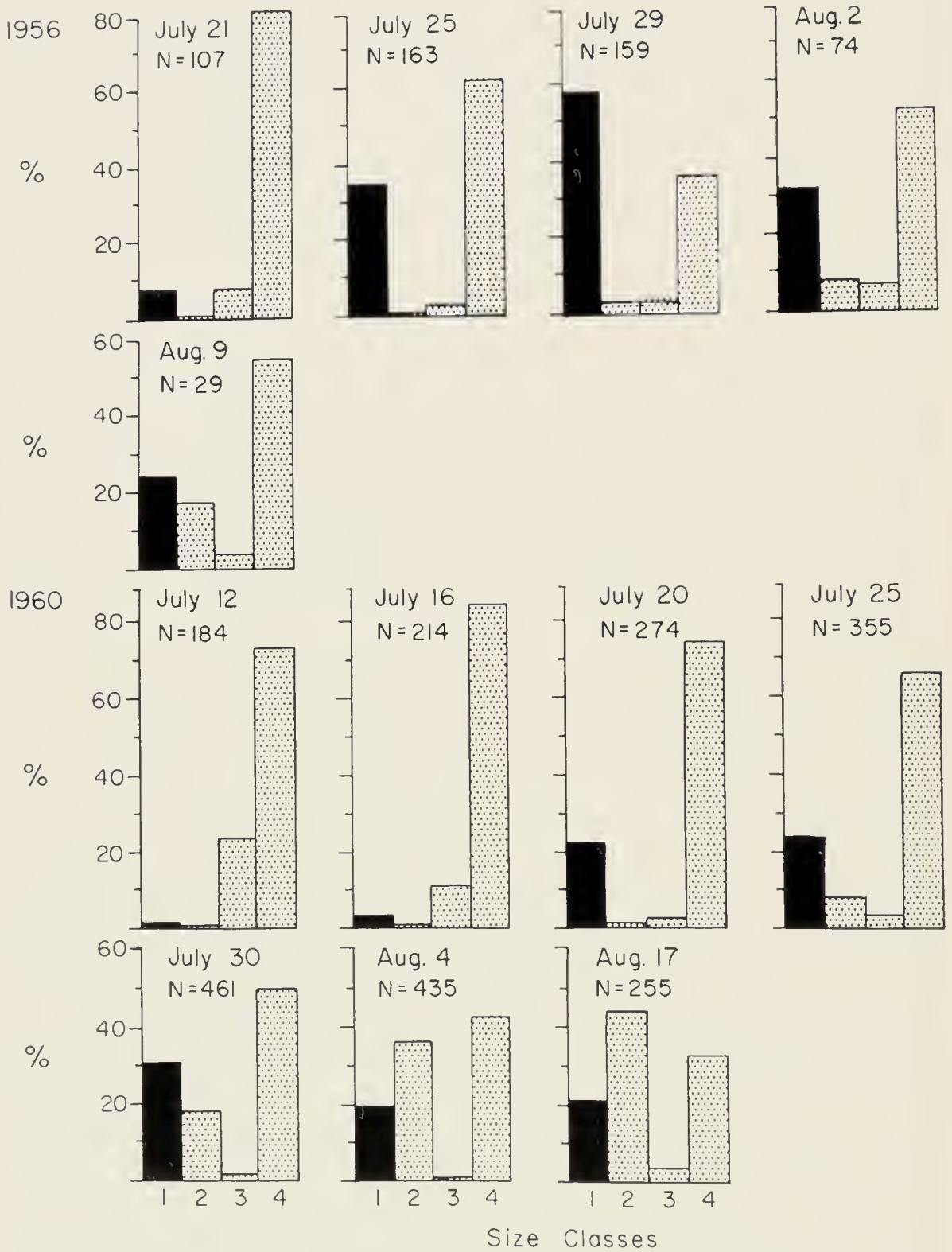


FIG. 4. Size classes of lemming femurs in penne jaeger chick pellets analyzed by short time intervals.

According to Thompson (1955a) young *Lemmus* leave the nest when about 12 g in weight, and are weaned at approximately 15 g. Size class 1 is probably newly weaned lemmings or nestlings. The average weight of size class 2 is about 25 g. In 1956 size class 1 was heavily represented (35 per cent of the total) and size class 2 very slightly represented (3 per cent); whereas in 1960 size class 1 was 20 per cent, and size class 2 was 19 per cent of total lemming prey.

The chick pellets were further analyzed by time intervals to compare seasonal trends in the age classes of prey taken (Fig. 4).

In both seasons adult lemmings were most of the prey in early July. Nestling or newly weaned lemmings, (size class 1) appeared in the jaeger chick pellets in the latter part of July and subsequently increased in importance. In 1956 however, size class 1 formed a far greater percentage of the total than in 1960, 58 per cent on 29 July 1956 vs 31 per cent on 30 July 1960. The difference suggests a comparatively heavy impact on this size class in 1956. Size class 2 appeared in the 1956 sample on 29 July and reached 17 per cent of the total prey by 9 August. In 1960 the same size class appeared in the 25 July sample and steadily increased to 36 per cent of the 4 August sample and 43 per cent of the 17 August sample.

The difference in the prey population in chick pellets in these two years is probably the result of difference in intensity of predation by Pomarine Jaegers in the two seasons. Figures have already been given (Table 3) on the very low reproductive success in 1956 and the very high success in 1960. It is assumed that food shortage and increased hunting intensity in 1956 resulted in a proportionately heavy take of small lemmings as soon as they were available and that the number taken was sufficient to reduce recruitment from size class 1 into size class 2 in that year. In 1960, on the other hand, food was abundant, and there was an ample number of adult lemmings available so that predation on the smaller size classes did not significantly impede recruitment into size class 2.

(2) *The number of prey taken.*—The amount of food eaten by captive chicks is used to estimate food consumption by wild chicks. The use of captive chick food data for this purpose can be justified by comparing the growth rates of the captives with the mean growth rate of penned wild chicks. Growth of Pomarine Jaeger chicks in the first ten days is almost constant. The mean instantaneous relative growth rate of two captive chicks in that period was 16.8 and 15.6 per cent. However, both captive chicks lost weight on their first day and had negative instantaneous relative growth rates from day one to day two. Since eight penned wild chicks had a positive mean instantaneous relative growth rate of 17.5 per cent from day one to day two, I assumed that the weight loss was due to inadequate feeding. If the first days weight loss is ignored the captive chicks had mean instantaneous relative growth rates for the first ten days of 19.5 and 18.0 per cent respectively, approximately the same as the 19.3 per cent for the penned wild chicks in the same age period in 1960 (Fig. 5). Both the weight curve of the successful chick Hotspur and the mean curve of the penned wild chicks leveled off at about 600 g.

The captive chicks were fed mostly on lemming carcasses and a few white mice, thus giving the total number of lemmings as well as the total weight of food eaten (Table 5). Most of the lemmings were entire although some were gutted.

Only one chick (Hotspur, Table 5) was raised from hatching to fledging age. In 47 days this chick ate 9,490 g of *Lemmus* or 202 lemming carcasses. The other chick raised from hatching (MaeDuff) died suddenly when 26 days old. There was no apparent cause of death, the chick began losing weight about 1 August and died three days later. In 26 days it consumed 3,521 g of *Lemmus* and ate 54 lemmings.

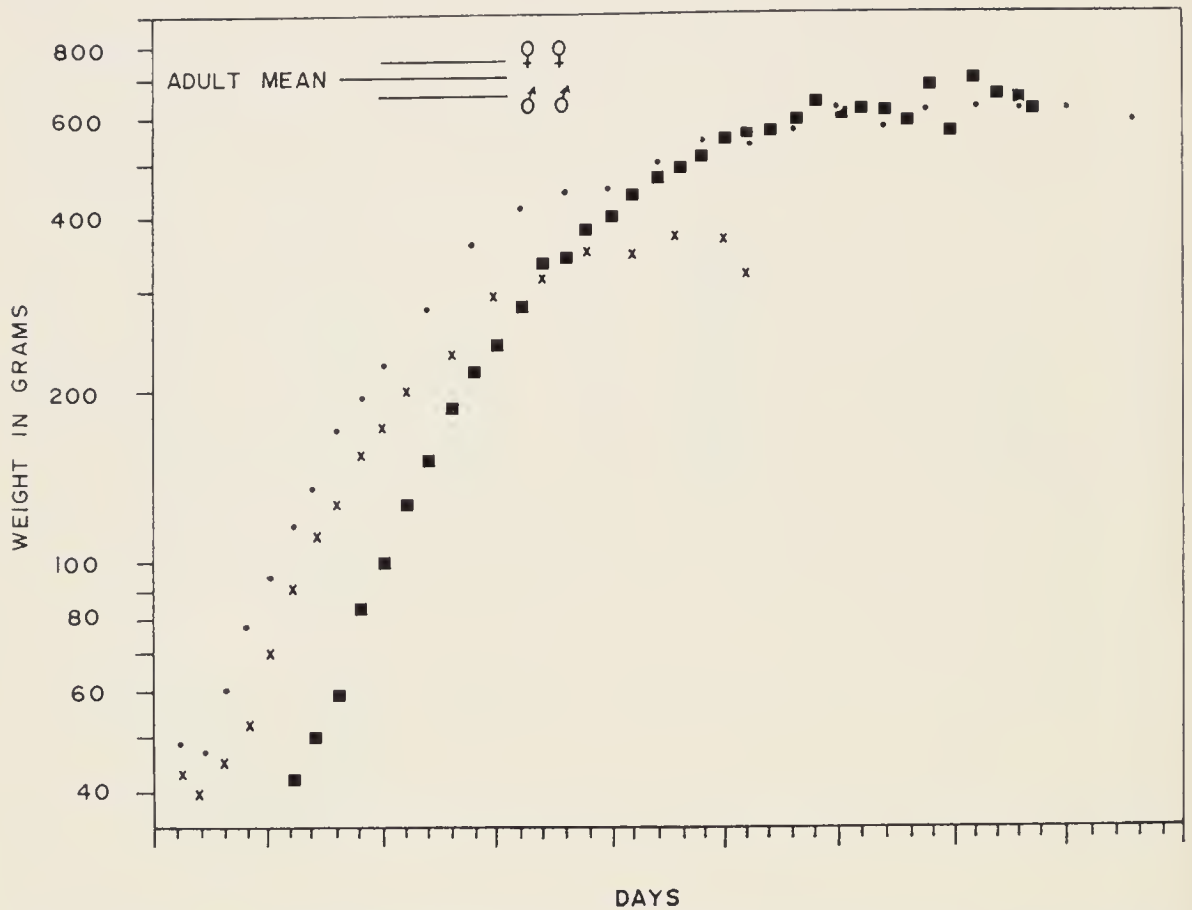


FIG. 5. Weight curves of two laboratory raised jaeger chicks (left) and the mean weight curve of penned jaeger chicks (right).

Two chicks near fledging weight kept for 24 and 28 days consumed an average of about 200 g or 5.5 lemmings per day.

These data suggest that a chick will eat about 9,500 g of food, or approximately 200 lemmings to grow from hatching to fledging. After reaching nearly full size a jaeger chick will eat 200 to 220 g of food per day, or 5.5 lemmings per day.

TABLE 5
AMOUNT OF FOOD CONSUMED BY CAPTIVE POMARINE JAEGER CHICKS IN 1960

Chick	Dates	Age (days)	No. of days	g food	g food/day	No. of Lemmus eaten	Mean no./day
Hotspur	11 July-3 August	1-24	23	3,671	160	54	2.3
	4-27 August	25-48	24	5,819	242	136	5.7
	Total	1-48	47	9,490	202	190	4.0
MacDuff	10 July-4 August	1-26	25	3,521	141	54	2.2
Cathy	4-27 August	??	24	5,105	213	136	5.7
Archy	31 July-27 August	??	28	5,550	198	151	5.4

TABLE 6
NUMBER OF LEMMINGS TAKEN BY POMARINE JAEGER PAIRS IN 24 HOURS

Date	Year	Male	Female	Total
7-8 July	1956	3	1-2	4-5
18-19 June	1960	3	8-9 ^a	11
7-8 July	1960	3.5 ^b	1.5 ^c	5
23-24 July	1960	2	2	4-5 ^d
13-14 August	1960	4 ^e	3	7

^a One lemming was torn apart but apparently only partly eaten.

^b Male caught and gutted two and was seen feeding on another lemming carcass. These were each counted as 0.5 lemming.

^c Female caught and ate part of one, was seen picking at carcasses twice. These were also each counted as 0.5 lemming.

^d The chicks were fed twice when the adults were not observed catching a lemming.

^e The male also caught one Red Phalarope, his total for the day was four lemmings and one phalarope.

One piece of information on the quantity of lemmings fed by a pair of adults to chicks was accidentally obtained in 1956. The female of a pair whose nest was fenced was dead near the nest on 22 July. The male was present, and the two chicks were still alive. There was no food in the nest enclosure. The following morning eight adult lemming carcasses were in the enclosure; that afternoon there were seven lemmings and one Steller's Eider chick (*Polysticta stelleri*). Normally, when one adult catches a lemming both fly to the enclosure and they cooperate in tugging the carcass apart so that both chicks and adults share the prey. In the absence of the female, this male was apparently unable to feed the chicks and the prey simply accumulated in the enclosure. The eight lemmings and one eider chick are a suggestion of the number of prey normally fed to two chicks if we assume that the male had eaten enough for himself. Lemmings in this part of the summer averaged about 50 g (Pitelka, MS). The food brought to the enclosure totaled about 450 g, allowing 50 g for the eider chick, and approximately equals the food consumed by the captive chicks.

The best information on lemming consumption by adult jaegers was obtained by observing breeding pairs for 24-hour periods in 1956 and 1960 (Table 6). The 24-hour watch made on 18-19 June and the two on 7-8 July, were in the incubation period and indicate approximately seven lemmings consumed by a pair of adults. The average weight of 107 lemming specimens from June and early July in 1956 was about 72 g (Pitelka, MS). The weight of seven lemmings eaten by one pair of adult jaegers in 24 hours was then about 500 g, or 250 g each. This seems very reasonable when compared with 200 to 220 g eaten by full sized chicks in captivity.

Two 24-hour watches made when chicks were being fed (23-24 July, and 13-14 August) indicated an average of approximately six lemmings consumed per pair. According to what we know of consumption rates of captive chicks this is much too low. It is possible that the presence of observers inhibited the adults from normal hunting activity or from visiting the chicks. Therefore the food consumption rate of 500 g per day per pair, determined for the first half of the season, was presumed to be constant for the entire season, and was also used as the adult consumption rate for the second half of the season.

The number of lemmings eaten by a successful Pomarine Jaeger family was calculated from these data on food consumption. Two chicks consume the equivalent of 20,000 g of

TABLE 7
SEX RATIO OF LEMMING PELTS FROM POMARINE PELLETS

Date	Males	Females	Per cent males	Per cent females	Totals
<i>1956. chick pellets</i>					
21 July	20	15	57	43	35
25	19	23	45	55	42
29	14	20	41	59	34
14 August	12	20	38	62	32
Total	65	78	46	54	143
<i>adult pellets</i>	104	118	47	53	222
Total	169	196	46	54	365
<i>1960. chick pellets</i>					
12 July	39	34	53	47	73
16	59	48	55	45	107
20	86	60	59	41	146
25	62	49	56	44	111
30	71	64	53	47	135
4 August	58	38	60	40	96
8	15	20	43	57	35
17	12	20	38	62	32
Total	402	333	55	45	735
<i>adult pellets</i>	33	33	50	50	66
Total	435	366	54	46	801

lemmings from hatching to 31 August. Using size class distribution of femurs in pellets as indicating the size classes of lemmings taken in that period (Fig. 3, Table 4), it was calculated that two jaeger chicks would have eaten 339 lemmings in 1956 and 319 in 1960.

The lemming consumption by adult jaegers was calculated for two time intervals. One interval from 25 May to 15 July is the period before the eggs hatch and before the young *Lemmus* of the summer generation emerge from the nest. (For the purpose of this analysis, these two events which were actually separated by a short interval, are assumed to occur simultaneously). The second interval from 16 July through 31 August, is the time from hatching to departure from the breeding grounds.

A consumption rate of seven lemmings per day per pair, derived from the results of these 24-hour watches, was used for the first half of the season, giving a total of approximately 364 lemmings taken. This is the equivalent of 500 g of lemmings per day. At this same rate of consumption for the second half of the season, taking into account the shift of the age structure of the lemming population (Fig. 3), a total of 413 lemmings were eaten in 1956 and 366 in 1960. Thus a pair of adults and two chicks eats approximately 1,050 to 1,100 lemmings in one season.

(3) *Sex ratio of lemmings taken.*—In assessing the impact of a predator on a prey population the sex ratio of the individuals removed is as important as the numbers and age classes.

The sex ratio of all prey pelves in both 1956 and 1960 was almost 1:1 (Table 7). Females predominated slightly in 1956 (54 per cent) and males were 54 per cent in 1960. The initial sex ratio in 1956 in the jaeger chick pellet samples favored males, and there was a continuous decline of the proportion of males through the season. Only in the first sample (21 July) did the percentage of males exceed that of the females. In 1960 the sex ratio in the June sample was 1:1. In July and early August samples it was predominantly male, and only in the 8 and 17 August samples did the percentage of females exceed that of the males. Considering the small size of the samples in 1956 we cannot be certain that the shift in the sex ratio is actually as steady as the data indicate, but a trend to a predominance of female prey is indicated in contrast to the results from 1960.

It is known that male lemmings, like other male microtines, range more widely than the females (Thompson, 1955a) and, hence, are presumably more exposed to predation than females are. This fact has been used to explain the predominance of males usually found in raptor pellets. The sex ratio of lemmings in Snowy Owl pellets from Barrow, for example, was 65 males to 35 females (Thompson, 1955a). The Pomarine Jaegers, however, may be obtaining a more random sample of the prey population than raptorial birds such as the Snowy Owl because they appear to use auditory cues in addition to visual cues to locate prey, because they dig their prey out of the ground, and because of their comparatively small territory.

Early in the season when lemmings are abundant and have little cover, jaegers hunt by flying over the tundra between 15 and 25 feet from the surface; and when a lemming is sighted the jaeger lands and grabs it with its bill. The feet are never used. After the ground thaws and after the shallow lemming burrows are open lemmings are less available, and jaegers obtain them primarily by digging them out of the peat soil with their bills. They appear to use both momentary sighting of a lemming and auditory cues to locate areas in which to dig. Two characteristics of northern Alaska coastal tundra make the second hunting method feasible. The surface layer of soil which thaws in the summer, the active layer, is very shallow. In marsh areas, which are the preferred habitat of *Lemmus*, it may be only six inches deep by late summer. Lemming burrows are therefore usually very shallow, in marsh peat they are typically just below the surface. Secondly, the vegetation is rarely more than five to six inches tall at the end of the growing season, and provides relatively poor cover for lemmings.

One other reason why the Pomarine Jaeger should obtain a more random sample of its prey population than the Snowy Owl and other raptors relates to the relative intensity of territory use. At high densities the Pomarine Jaeger has a relatively small territory, approximately 34 acres on the average, and particularly early in the season, it is confined to that area for all of its food gathering. The jaegers hunting effort for an entire season must be intensive, and its prey should ultimately reflect the actual sex ratio of the prey population.

The Snowy Owl, on the other hand, occupies a much larger area, one square mile or more, and does not have to harvest prey as intensively as the jaeger does. The owl apparently relies on visual cues to locate prey and will in the long run probably take more of those lemmings, the males, which are more active on the surface.

The difference in the sex ratio of the jaeger's total prey between 1956 and 1960 is probably explained by different intensity of predation in the two years, as a result of the difference in the number of lemmings present. In 1960 lemmings were plentiful through the season. With a readily available food supply one would expect the jaegers to take a predominance of the more active lemming sex, the male. In 1956 a shortage of lemmings

developed, and hunting was intensified as indicated by a large amount of time that jaegers spent in hunting activities such as walking and digging. Under this hunting pressure the prey taken should tend to reflect the ratio in the population or perhaps even become selective for females. Increased predation of females under these circumstances should result because in the reproductive period the females have nests of young, either on the surface of the ground or in chambers excavated just beneath the surface. A tendency to defend a nest or to remain with the young should increase the chance that a randomly encountered female would be taken by a jaeger over the chance that a similarly encountered male would be taken.

(4) *Timing of predation.*—The lemming population is free of avian predators for the first one and three-quarter to two and three-quarter years after a decline. Avian predators may breed in low to moderate numbers in the third summer following a decline. Little is known of the least weasel in this period; it is rare and never seen or captured except in peak lemming years. Presumably it is an important factor only in the last year of the cycle.

In a lemming-high summer, jaegers are significant as predators on the lemmings for a little more than three months, from late May until the end of August. Snowy Owls arrive earlier, in late April, and are important predators until the end of August, for four and possibly more months. They have been known to winter in areas of high rodent population and so could have a more prolonged effect than any other avian predator. The Short-eared Owl is sporadic in its occurrence in northern Alaska and has not nested in numbers at Barrow since 1953. The Glaucous Gull occurs in moderate numbers along the north Alaskan coast all summer. In lemming years it is seen taking lemmings during spring melt-off. In that brief period the species probably has a significant effect on the lemming population near the coast. The Parasitic Jaeger is relatively scarce at Barrow and is primarily a bird predator. In 1956, a high lemming year, one pair appeared to feed mostly on fish.

Lemmings are most vulnerable to predation in early spring; they have destroyed their vegetative cover, the only remaining cover, the snow, melts rapidly, and their burrow systems remain frozen or full of water and are unusable. Lemmings are so easily taken in spring that some waste by the predators is evident. Thompson (1955a) found 11 to 12 dead lemmings per acre on several mortality plots in June 1953. More than half of these bore the marks of owls, jaegers or weasels. Though most of the wasted animals are eaten eventually, some are probably lost, thus increasing the total removed by the predators.

A large number of Pomarine Jaegers which eventually depart without breeding add to the impact of predation in early spring. The number of excess birds differs considerably between high years. In 1956 excess birds were estimated to be equal to 25 to 50 per cent of the final breeding population, and in 1960 they were estimated to be less than 25 per cent of the breeding population. In 1952 Pitelka (1955a) estimated that excess birds numbered five times the number of breeding birds.

The impact of a pair of breeding Pomarine Jaegers on the lemming population is constant until the eggs hatch in mid-July. Food consumption then increases as the chicks are fed. Consumption by the chicks, and hence by the entire family, peaks when chicks are in their third week and then declines slightly. Young *Lemmus* emerge from the nest in mid- to late July, adding a large number of small lemmings to the prey population when jaeger chicks are

TABLE 8
 TOTAL PREDATOR IMPACT ON A HIGH LEMMING POPULATION AT BARROW

Predator	Age class	Density (Ind./square mile)	Daily food consumption (g/ind.)	Seasons lemming consumption			Total
				(per ind.)	(per acre)		
					25 May to 15 July	16 July to 31 August	
Pomarine Jaeger	Adult	38	250	338	10	21	31
	Young	38	200	167	—	—	
Snowy Owl ^a	Adult	2	250	350	1.3	1.6	3
	Young	7	150	160	—	—	
Least weasel ^b		64	50	100	5	5	10
Glaucous Gull ^c		20	250	125	0.7	—	1
Waste					4	—	4
Totals					21	28	49

^a Data from Watson, 1958.

^b Data from Thompson, 1955*a*.

^c Estimated.

hatching or partly grown; hence, the number of lemmings consumed increases at a proportionately greater rate than the weight of food consumption would indicate.

Predator impact on a lemming high.—I have used the information on food habits to assess the effect of a high Pomarine Jaeger population on lemming numbers in a year such as 1956 or 1960 at Barrow. I have also tried to define the total predation impact by estimating the effect of the other lemming predators (Table 8). Data for food consumption of the Snowy Owl are from Watson (1958). The density of the least weasel is that given by Thompson (1955*a*) for the 1953 season; it is a conservative estimate. Data on Glaucous Gull density are from my own observations; the food consumption of the gull was estimated on the basis of its weight. The estimate of lemmings wasted was from Thompson (1955*a*) for the 1953 lemming high, allowing for the lower lemming population in 1956 and apparent lack of waste in 1960.

The figures in the three right columns of Table 8 are estimates of predation on a single acre of tundra by each of these predators. The number of lemmings consumed are for two halves of the season, for reasons already discussed, with the season's total in the right column. All predation figures are based on numbers per area without adjustment for unoccupied habitat, and thus are the lowest mean densities for the species involved.

The Pomarine Jaeger takes 31 (63 per cent) of the 50 lemmings removed

TABLE 9
HYPOTHETICAL EFFECTS OF PREDATION ON HIGH LEMMING POPULATIONS OF
DIFFERENT SPRING DENSITIES

Lemming density based on individuals per acre			
Spring density/acre	20-30	30-40	40-50
Number of females	12.5	17.5	22.5
Females lost before breeding	10.5	10.5	10.5
Females left to breed	2	7	12
Average embryos	6 ^a	6	6
Young produced	12	42	72
Total adults remaining	4	14	24
Total mid-summer population	16	56	96
Predation loss after breeding	28	28	28
Excess after predation	-12	28	68

^a Datum from Thompson, 1955a.

per acre by all predators. Its great importance as a lemming predator is thus clearly demonstrated.

I have used three broad estimates of spring lemming numbers per acre: 20-30, 30-40, and 40-50 to assess the effect of predation on the summer lemming population, using the impact of minimum predator density in Table 8. The results (Table 9) are a mean minimum figure for the impact of predation, and suggest that total predator load can depress a spring lemming population of approximately 25 per acre but cannot depress a spring lemming population of 35 per acre or above. The results also indicate the decisive effect that predation in the first half of the summer has on subsequent lemming numbers. Early removal of a relatively few females from the population can mean the difference between a reduction of the lemming population in the summer or not, thus emphasizing the importance of a predator like the Pomarine Jaeger which apparently takes a greater proportion of females than do other avian predators.

These calculations indicate that the predation load on the lemming population is significantly large and can depress lemming populations of some densities, thus confirming the observation that the lemming population was indeed depressed markedly in one high year (1956) and not in another (1960) (Pitelka, MS).

The possible effect of predation by the excess jaegers always associated with breeding populations in spring has not been included in the estimate of total predation load. I have no precise data on their numbers, but their impact can be estimated if we assume there are as many as 25 to 50 per cent of the maxi-

mum breeding population and that they are present in the population for ten days. Under these circumstances they would add 0.5 to 1.0 lemmings per acre to the early season predation impact, and reduce the fall lemming population by two to three lemmings per acre. Assuming they were present as long as 20 days would reduce the fall lemming population by three to six lemmings. These figures do not suggest that this extra spring predation is significant in the total predation load; but it could be pivotal in some years.

Lemming mortality from causes other than predation has been ignored in this discussion. Thus, lemming nestling mortality from action of intraspecific factors, spring flooding, and exposure probably account for some additional mortality; and disease and parasitism while not significant (Krebs, 1964) also remove a few.

This argument has been based on a hypothetical population of jaegers with 100 per cent reproductive success. In fact, success is never that high. Yet, the most decisive part of the season as far as impact on the lemming population is concerned is the first half; and in 1956, a very unsuccessful season for the jaegers, most of the pairs which began to breed were still present in mid-July. The decline of the jaeger population did not take place until the late July when food shortage and consequent chick starvation began to occur. Hence, even in a year when the breeding effort of the predators fails, they may have a critical effect on the prey population by their impact before its summer breeding.

DISCUSSION

The role of predation in the lemming cycle.—Most modern students of the lemming cycle reject the idea that the cycle is caused by predators (Krebs, 1964). Predators do kill a large number of lemmings, and Pitelka, Tomich, and Treichel (1955a) suggested that under some circumstances predators could affect the periodicity of the cycle by postponing a population peak from one season to the next. They suggested that in a summer of moderate lemming numbers, in 1952 at Barrow, the predators prevented the lemmings from increasing and postponed the lemming population peak to the summer of 1953.

Current hypotheses are concerned with causative factors intrinsic to the lemming population (Christian, 1950; Chitty, 1952) or are concerned with interaction of the lemming population with its food supply (Lack, 1954; Pitelka, 1957). However, Pearson (1966) studied the effectiveness of mammalian predators on a complete cycle of abundance of *Microtus californicus* and concluded that carnivore predation was "an essential part of the regular cycles of abundance of lemmings, *Microtus*, and other microtines."

According to Pearson mammalian predators are not necessarily important in starting the decline from the population peak, but are important in reducing

the population to the lowest part of the cycle and in maintaining the low population until they themselves starve. Their action accounts for one of the most inexplicable aspects of the lemming cycle; the long delay in recovery from the population low.

Since avian predators are not present in significant numbers during the lemming population build up, their role in the cycle in northern Alaska is practically restricted to their action on the lemming peaks. The evidence presented here shows that avian predators do take a large number of lemmings and that at some lemming densities they can markedly depress the lemming population, while in others they cannot. There is also observational evidence that lemmings may be reduced in numbers by avian predators (1956), or they may increase despite the action of avian predators as in 1960. The events of 1956 demonstrated dramatically that the avian predators cannot be responsible for a complete lemming decline as in that year most of the jaeger chicks starved when it was still possible to snap trap some lemmings. The role of the avian predators in the lemming population cycle in northern Alaska then seems to be the exploitation of the peak population and to truncate the top of the peak by their action.

The role of mammalian predators in the lemming cycle in northern Alaska has not been studied; but the large population of least weasels which occur in the peak summer must persist into winter, and since there is no alternative prey, they must continue to prey on the lemmings remaining after the avian predators depart. Arctic foxes are also usually abundant at the end of lemming-peak summers. They are not usually seen near Barrow in the summer, but in autumn numbers of young of the year are seen apparently foraging for lemmings. Thompson (1955*b*) interpreted the results of his study of the lemming population from 1950 to 1954 at Barrow as being best explained by Lacks' (1954) food hypothesis. Yet he also says (Thompson, 1955*b*, p. 173) that "our field evidence strongly suggests that it is the continued pressure by weasels through the winter which eventually reduced the lemmings to the extremely low numbers of 1950 to 1954. As lemmings declined in abundance, the owls, jaegers, and foxes emigrated and shifted to other food, but the weasels' only alternative was to extend their efforts in pursuing the remaining lemmings." Maher (1967) presented evidence that a low to moderate winter population of lemmings was almost destroyed by predation by ermine on Banks Island, N.W.T. These observations strongly suggest that predation, particularly by weasels, may in fact be responsible for the great decline of lemmings in the winter after a peak summer in northern Alaska, and thus may be causing the population cycle.

Evidence from the eastern North American arctic is not as suggestive, but

both Krebs (1964) and MacPherson (1966) working in areas where the two lemming species (*Lemmus* and *Dicrostonyx*) occur together in a mosaic of habitats which bring them in close proximity found that their populations cycled synchronously. Synchrony of the two species suggests some external action tending to keep them in phase, and predation by mammalian predators is a very possible responsible factor, although Krebs (1964) rejected this possibility.

The possibility that the action of mammalian predators in reducing the population and prolonging the low is responsible for the cycling of the lemming population now seems tenable and should be studied further.

SUMMARY

Food habits, breeding density, and breeding success of Pomarine Jaeger populations nesting in response to different spring densities of the brown lemming population were studied at Barrow, Wainwright, Pitt Point, and Cape Sabine, northern Alaska. Food habits of nonbreeding populations were studied for comparison with breeding populations.

When Pomarine Jaegers breed, their food supply is at least 80 per cent lemmings with birds the next most important food category. Lemmings occurred in less than half of the stomachs of nonbreeding populations, suggesting that the jaeger cannot obtain enough food to support breeding unless there are enough lemmings to provide most of its food.

Jaeger breeding density correlated with spring density of the brown lemming up to a maximum density of approximately 19 pairs per mile. Three lemming highs (1953, 1956, and 1960) supported virtually identical mean Pomarine Jaeger densities although lemming density differed between peak years.

Breeding success was low at low breeding densities and low to moderate at intermediate densities. At maximum density, breeding success ranged from almost complete failure (1956) to high success (1960).

The size classes of lemmings in the jaegers' diet was determined from the length of femurs in regurgitated food pellets of adults and chicks. The number of prey taken was determined by the amount of food eaten by chicks raised in the laboratory, and by several 24-hour watches of jaeger pairs. The sex ratio of lemming prey was determined from the pelvis in jaeger pellets.

Calculations from these data indicate that a pair of jaegers raising two chicks in a year of maximum jaeger density remove an average of 31 lemmings per acre from their territory in the season. Other predators remove an additional 18 for a total of 49 lemmings removed per acre by the action of all predators. This is sufficient to depress a lemming population of approximately 25 per acre in the spring but not a population of 35 per acre or above.

The role of the avian predators in the lemming cycle is to truncate the peak populations, but they are unable to reduce the lemming population to the low point of the cycle. It is suggested that mammalian predators, especially *Mustella rixosa*, are responsible for reducing the population completely and delaying recovery of the lemming population until they themselves decline in numbers.

ACKNOWLEDGMENTS

Financial support for the field portion of this project was provided by the Arctic Institute of North America under contract with the Office of Naval Research. Logistic support

was from the Arctic Research Laboratory at Barrow, Alaska. The assistance of these agencies is gratefully acknowledged.

I am grateful to Frank A. Pitelka for advice in the course of this study.

I also wish to thank Ira L. Wiggins, Director of the Arctic Research Laboratory in 1956, and Max C. Brewer, his successor, for their generous support of my field activities.

Many investigators and staff members at the Arctic Research Laboratory have generously provided information and time to this project. I regret that I cannot express appreciation for all of those contributions. I particularly thank: J. Dow, R. T. Holmes, M. P. Marsh, F. A. Pitelka, J. Reynolds, and T. Sovalik.

Dow helped map the Pomarine Jaeger nests in 1956, Holmes and Reynolds helped in 1960. Holmes, Marsh, Reynolds, and Sovalik assisted in several 24-hour watches of Pomarine Jaegers in 1956 and 1960.

Grateful acknowledgment is made of facilities and support provided by the Museum of Vertebrate Zoology and the Department of Zoology of the University of California, Berkeley.

LITERATURE CITED

- BENT, A. C. 1921. Life histories of North American gulls and terns. U. S. Natl. Mus. Bull., 113.
- BLACK, R. F., AND W. L. BARKSDALE. 1949. Oriented lakes of northern Alaska. J. Geol., 57:105-118.
- BRITTON, M. E. 1957. Vegetation of the Arctic tundra. Eighteenth Ann. Biol. Coll., Oregon State College, pp. 26-61.
- CHILDS, H. E., JR. 1959. Vertebrate ecology of coastal tundra in northwestern Alaska. Unpubl. Ph.D. thesis, University of California, Berkeley.
- CHITTY, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-39. Phil. Trans. Royal Soc. London, Ser. B, Vol. 236:505-552.
- CHRISTIAN, J. J. 1950. The adrenal-pituitary system and population cycles in mammals. J. Mammal., 31:247-259.
- DUNMIRE, W. W. 1955. Sex dimorphism in the pelvis of rodents. J. Mammal., 36:356-361.
- KREBS, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959-62. Arctic Inst. N. Amer. Tech. Paper No. 15.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford.
- MACPHERSON, A. H. 1966. The abundance of lemmings at Aberdeen Lake, District of Kcewatin, 1959-63. Canadian Field-Naturalist, 80:89-94.
- MAHER, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. Canadian Field-Naturalist, 81:248-250.
- PEARSON, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. Anim. Ecol., 35:217-233.
- PITELKA, F. A. 1957a. Some characteristics of microtine cycles in the arctic. Eighteenth Ann. Biol. Coll., Oregon State College, pp. 73-88.
- PITELKA, F. A. 1957b. Some aspects of population structure in the short-term cycle of the brown lemming in northern Alaska. Cold Spring Harbor Symp. Quant. Biol., 22: 237-251.
- PITELKA, F. A., P. Q. TOMICH, AND G. W. TREICHEL. 1955a. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Monogr., 25:85-117.

- PITELKA, F. A., P. Q. TOMICH, AND G. W. TREICHEL. 1955*b*. Breeding behavior of jaegers and owls near Barrow, Alaska. *Condor*, 57:3-18.
- RAUSCH, R. 1950. Observations on a cyclic decline of lemmings (*Lemmus*) on the arctic coast of Alaska during the spring of 1949. *Arctic*, 3:166-177.
- SHELFORD, V. E. 1943. The abundance of the collared lemming (*Dicrostonyx groenlandicus* (Tr.) var. *richardsoni* Mer.), in the Churchill area, 1929 to 1940. *Ecology*, 24:472-484.
- SPETZMAN, L. A. 1959. Vegetation of the arctic slope of Alaska. U. S. Geol. Surv. Prof. Paper 302-B.
- THOMPSON, D. Q. 1955*a*. The ecology and population dynamics of the brown lemming (*Lemmus trimucronatus*) at Point Barrow, Alaska. Unpubl. Ph.D. thesis, Univ. of Missouri.
- THOMPSON, D. Q. 1955*b*. The role of food and cover in population fluctuations of the brown lemming at Point Barrow, Alaska. *Trans. N. Amer. Wildl. Conf.*, 20:166-176.
- THOMPSON, D. Q. 1955*c*. The 1953 lemming emigration at Point Barrow, Alaska. *Arctic*, 8:37-45.
- WATSON, A. 1958. The behaviour, breeding, and food-ecology of the Snowy Owl *Nyctea scandiaca*. *Ibis*, 99:419-462.

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